THE ENERGETICS OF POLLINATION

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Many animals derive their food energy from the nectar of flowers, and the flowers may also provide them with the materials for growth and reproduction. To the plants, in turn, the animals are the vehicle for the transport of male gametes for fertilization. As a consequence, there is a mutual interdependence involving a set of evolved "games" where the pollinators try to get the most for their foraging effort, while flowers provide the least reward possible. The flowers must provide enough reward to attract the pollinators and keep them from visiting competitor species, but the rewards must be sufficiently small to keep them moving from one plant to another (Heinrich & Raven, 1972). Interesting complications arise in this simple scheme in male vs. female functions of flowers, when manyflowered vs. few- or single-flowered plants are considered, and when any one plant's most potent competitors are other individuals of the same rather than other species. The latter aspects have been little explored. In order for the pollination system to "work" requires several conditions. First, there must be advertisement of the rewards. Secondly, flower morphology must be appropriate for the pollinator to become dusted with pollen without dusting the pistil, and to transfer this pollen to a receptive pistil of another flower. The morphological features of the flower act to manipulate the close-in behavior of the pollinator to increase the percentage of cross-pollination events per given food reward provided, or per given forager-flower encounter (Macior, 1974). It is probably a safe working hypothesis that the foragers have selected, by those visits that have resulted in fertilization, most of the flowers that we know today. They have been the agents of flower horticulture in nature, and if we want to observe the selective pressures that have shaped or are shaping flower evolution, we must look to the foraging behavior of the flower visitors. The third major consideration is that the foragers must not only be appropriately manipulated at the flowers, they must also be caused to move between them (Heinrich & Raven, 1972). This involves energetics. And when one looks from the standpoint of energetics, it becomes necessary to consider the environment and the other plants relative to whom the pollinator's choices are made. Most pollinators are inherently promiscuous; they visit flowers for the rewards they contain, regardless of the shape or color of the flower's exterior. But to the plant, to whom flower constancy is important for cross-pollination, fidelity can be "bought" by providing large food rewards. But this purchase may be at a high price. In the immediate, ecological, sense, too strict a fidelity will hinder the contribution of male gametes to other flowers. A bee, for example, will return repeatedly to a single blossom, visiting no others, provided this blossom is sufficiently rewarding, conspicuous and isolated (McGregor et al., 1959). A second cost, one that may not be apparent unless measured against an evolutionary time

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span, is that calories used to feed pollinators are no longer available to be thrown into fruit and seed production.

The energetics of pollination is now an old topic. It is at least eight years old. In the last several years, a flood of excellent research has been published. The foraging behavior of many kinds of nectivores has been explored (Heithaus et al., 1974; Heinrich, 1979a, 1979b; Howell, 1979). Ecological studies have examined the important role of the pollinator's competition for food resources in shaping various plant communities (Moldenke, 1975; Inouye, 1978; Ostler & Harper, 1978; Schemske et al., 1978; Moral & Standley, 1979). Many studies on the foraging behavior in the field in various parts of the world have been aimed, in part, to gain insights into ecology and evolution (Macior, 1974; Willson & Rathke, 1974; Stiles, 1975; Carpenter, 1976; Frankie et al., 1976; Regal, 1977; Feinsinger, 1978; Silander & Primack, 1978; Sussman & Raven, 1978; Waser, 1978a, 1978b; Ford, 1979). It is not possible for me here to more than briefly mention a very small portion of the work that has been done. My aim will be to provide several contrasting examples illustrating different concepts, and to point out what these suggest in regard to new and productive research.

INTERSPECIFIC COMPETITION AND FLOWERING DIVERGENCE

An implicit early assumption in pollination energetics was that the energy balance between pollinators and the food rewards of flowers, which provides the selective pressure both to improve foraging efficiency and flower evolution, was competition. There is now a general concensus in the majority of recent papers on the theme of energy balance in pollination ecology that plants compete for pollinators, and that pollinators compete for plants. However, what is not always distinguished is whether one is dealing with the ecological or evolutionary time scales. Also, it must be recognized that perhaps in the ecological context and particularly in the evolutionary context, both competition for and between pollinators may be occurring simultaneously; all of the pollinators may be competing for the nectar provided by the highest nectar producers, while the lowest nectar producers may remain unpollinated. Relatively few papers have so far been addressed to intraspecific competition and the energy investment of plants in this competition to total flowering as well as to nectar production (but see Willson & Rathke, 1974; Silander & Primack, 1978; Schaeffer & Schaeffer, 1979).

Competition between pollinators is inferred from the fact that nectar is a highly-prized resource that is generally removed from flowers, by any of a variety of pollinators, soon after it becomes available. Secondly, the numerous intricate behaviors and specialized morphologies of nectivores that have evolved for foraging suggest that these animals have been under long selective pressure to per-fect their foraging techniques. If pollinator populations are limited by food supplies, then they should increase until all the available resources are utilized, and the different kinds of flowers are each visited in proportion to the food rewards available from them. Until the pollinators reach saturation densities, the most highly rewarding species may thus receive adequate pollination service, while the remainder, with relatively less net food rewards, may remain unpollinated, unless they shift their blooming to a less crowded time. "Cornucopian species" such as *Salix* spp. and *Taraxacum officionale*, for example, may disproportionately at-

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tract insects, causing these pollinators to abandon other spring flowers (Mosquin, 1971). Similar competition between species in the natural habitat is one proposed mechanism for the evolution of sequential blooming. Waser (1978a, 1978b) has recently pointed out, however, that "because a preferred species suffers no reproductive loss when flowering with a less attractive species, it should lengthen its flowering period in the absence of other constraints until it has completely excluded the less attractive species from the community or completely overlaps with it in flowering time." He proposes, instead, that a second, probably more ubiquitous, mechanism of competition for pollination involves loss of viability

from interspecific pollen transfer.

Waser (1978a) has shown that when the two common perennial plants, Delphinium nelsoni Greene (Ranunculaceae) and Ipomopsis aggregata (Pursh) V. Grant (Polemoniaceae), grow together in the dry meadows in the Elk Mountains of Colorado, they generally flower sequentially. The respective blue and scarlet flowers are commonly visited by broad-tailed hummingbirds (Selasphorus platycercus Swainson), and during the brief period of overlap in flowering of the two plants, the hummingbirds visit both species, carry mixed pollen from both species, and cause interspecific pollen transfer. Flowers of both species during this time of overlap in blooming, as well as potted plants subjected by hand to interspecific pollination, suffer significant (25–50%) seed set reduction relative to the nonoverlap period. This is excellent evidence that the two species compete for hummingbird pollination by way of competitive interaction of the interspecific pollen transfer, and Waser concludes that the reproductive loss of the plants in the period of flowering overlap represents a potent selective force that could maintain divergent flowering times of D. nelsoni and I. aggregata. The penalty of overlapping blooming in the unrelated perennials studied by Waser was a reduction in fertility, but in some closely related species the penalty can be still greater. For example, 36 species of annual plants, the clarkias (Onagraceae), grow in semiarid areas of California, and frequently bloom at the same time (MacSwain et al., 1973). These bee-pollinated annuals are vegetatively similar, but their flowers have petals of strikingly different shapes and color. Why have they evolved such different visual signals? Detailed studies of the foraging behavior of bees in the ecological context of different clarkia flowers have not yet been done. We can speculate, however, that since the flower fidelity of bees is based on conditioning to specific signals, then if the different species had similar flower signals the bees would be inconstant. Since clarkia hybrids are sterile, such inconstant foragers would predictably cause mass sterilization in their wake. Variety could thus have evolved to minimize straying. The variety, along with habitat differences and flowering time differences, may now be sufficient to have greatly reduced and perhaps even eliminated this lethal effect of competition. The selective pressure for flower divergence may or may not still be available for our inspection in the *natural* population.

CONSTRAINTS AND CONVERGENCE

A recent study of another group of co-occurring, mostly unrelated plants pollinated also by highly promiscuous pollinators shows, in contrast to the above two examples, a high degree of *convergence*. As previously described by Grant

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& Grant (1968), hummingbird-pollinated flowers in western North America are characterized by striking convergence in shape and color. Brown & Kodric-Brown (1979) made a detailed analysis of this pollination system in the White Mountains of Arizona. In this area they observed nine plant species, Ipomopsis aggregata (Polemoniaceae), Penstemon barbatus (Scrophulariaceae), Castilleja integra (Scrophulariaceae), C. austromontana, Lonicera arizona (Caprifoliaceae), Aquilegia triternata (Ranunculaceae), Silene laciniata (Caryophyllaceae), Echinocerus triglochidiatus (Cactaceae), and Lobelia cardinalis (Campanulaceae). All of these plants have long overlapping blooming time. The flowers of all species are red, have long tubular corollas, and frequently bloom in the same local habitat. All of these flowers were visited indiscriminately in the sequence and proportions in which they were encountered, by at least two common hummingbirds, Selasphorus rufus and S. platycerus. (Six additional species of hummingbirds overlap geographically with the range of most of the flowers.) With one exception (L. cardinalis) to be discussed later, all of the plants also supply similar nectar rewards. Since the close relatives of the plants have strikingly different appearance and are insect-pollinated (Grant & Grant, 1968), the similarities of the different genera must represent a true convergence, either by way of demography or by "coevolution." What have been the selective pressures for convergence and what mechanisms allow it to exist? These temperate hummingbirds are migrants, and Grant (1966) pointed out that it would be advantageous for all of the hummingbird-pollinated plants in the birds' migratory ranges to employ similar signals and rewards to attract whatever hummingbirds are locally available. A bird conditioned to find rewards at a specific kind of flower would be attracted to flowers of similar appearance at another locality. However, hummingbirds are relatively promiscuous flower visitors, so that there are probably other, more primary reasons. Brown & Kodric-Brown (1979) suggest also that these temperate hummingbirds are intra- and interspecifically territorial so that only one resident bird is reliably present within a local area. There does not appear to be a compelling reason to suppose, however, that this bird could not visit differently appearing flowers. I suggest, instead, that since these pollinators are migrants, they must be generally opportunistic feeders capable of visiting many types of flowers. Unlike resident tropical hummingbirds that differ greatly in bill shape and size (Stiles, 1975; Wolf et al., 1976; Feinsinger, 1978; Feinsinger & Colwell, 1978), the eight potential hummingbird pollinators of the nine plant species are unspecialized and not trophically separated from each other. However, a hummingbird's method of foraging is a relatively specialized behavior in its own right. It may have its own unique constraints, giving few evolutionary options to the plant. First, the high energy expenditure necessitates a high reward. The high nectar reward, in turn, necessitates a long tubular corolla to guard the nectar from nonpollinators. The red color also acts as a nectar guard in rendering the flower relatively invisible to insects while providing a vivid contrast against the foliage to the birds (Grant, 1966; Raven, 1972). A vivid visual display may be particularly important to attract these migratory pollinators from a distance.

There are severe constraints on the architecture of a high-reward flower that is pollinated by a hoverer outside the flower. But the positioning of the stamens

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and pistils within the flowers are not so severely constrained, and this suggests that flowers might use different parts of the hummingbird head to transport pollen. (If the same part of the head were used, there would potentially be a high percentage of interspecific pollen transfer that might result in the aforementioned loss of fertility observed in D. nelsoni and I. aggregata.) In the convergent hummingbird-pollinated flowers, P. barbatus and C. integra have dorsally located reproductive structures and they place most of their pollen on the crown and top of the bill, whereas I. aggregata, which has ventrally located anthers and stigma, deposited its pollen primarily on the chin. Where C. confusa bloomed together with P. barbatus, it deposited its pollen at the base of the bill and front of the crown, whereas the P. barbatus pollen was carried farther back on the head (Brown & Kodric-Brown, 1979). Although using different parts of the body as pollen-attachment sites might work with birds, it cannot work with equal impunity in bees (except with firmly attached pollinia as in Orchidaceae and Asclepiadaceae) that groom pollen from most parts of their body with their legs during successive flower visits. Nevertheless, as indicated by Macior (1974), bumblebee-pollinated plants also partition pollen. Bumblebee foragers do not completely remove pollen from the mid-dorsal and mid-ventral lines of the thorax, and numerous bumblebee-pollinated flowers are specialized to deposit pollen in these specific body parts (Thien & Marks, 1972; Macior, 1974). Indeed, as suggested by Macior (1974), the zygomorphic shape of many flowers (which acts to "guard" the nectar) may be an adaptation to confine and guide the pollinator over the reproductive parts, thus resulting in less wastage of pollen, providing another possible reason for flower convergence.

EXCLUSIVE SPECIALISTS AND INTERSPECIFIC COMPETITION

Unlike hummingbirds, bees tend to be highly flower-constant, and they do not forage in one relatively predictable way such as by hovering in front of a flower. They land on or enter flowers and collect nectar and pollen by different techniques as required by flower architecture (Macior, 1974; Heinrich, 1976). For example, to collect pollen from wild carrot, Daucus carota (Umbelliferae), bumblebees walk rapidly across the flat inflorescence, pressing their body down to pick up the pollen from the surface of the many tiny florets. In order to collect pollen from wild rose, Rosa sp. (Rosaceae), they press groups of anthers between thorax and abdomen, vibrate them, turn and grasp another group of anthers, and continue this procedure around the circular perimeter of the flower. To collect pollen from timothy grass, Phleum pratense (Poaceae), the bees simply scramble up an inflorescence, easily knocking off the loosely held pollen that then adheres to the body hairs. During each interfloral flight, the pollen is groomed from the body and transferred to the corbiculae. To collect pollen from blue bindweed, Solanum dulcamara (Solanaceae), the bees must grasp the hanging flowers with their mandibles and shake the pollen out of the tubular anthers onto the venter (see review, Heinrich, 1979c).

Nectar collecting by bumblebees also involves specialized behavior that is learned by individuals that remain relatively flower-faithful as long as rewards remain available (Heinrich, 1979a).

In order to collect nectar from "open" flowers, such as those of composites,

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requires little skill. But to enter a turtlehead, *Chelone glabra* (Scrophulariaceae), flower a bee has to pry apart the partially closed lips of the corolla and crawl deep into the flower and probe near the base of the pistil and the anthers. To collect nectar from jewelweed, *Impatiens biflora* (Balsaminaceae), the individual bee, depending on whether it is a short- or a long-tongued species, may get the nectar by biting into the nectar spur or by entering the flower from the front entrance. In monkshood, *Aconitum* sp. (Ranunculaceae), the ample nectar is held in specialized cuplike nectaries at the tips of modified petals. The nectaries are hidden under a hood of petallike sepals, and only some of the individual bees that

encounter these blossoms manage to find this nectar. Those that do find it are highly rewarded and remain highly flower-constant.

Even though any one species of bumblebee may collectively visit a very large range of different kinds of flowers throughout the season and at any one time within a season at a given site, the individuals are relatively flower-constant. By specializing to manipulate the "difficult" flowers, they gain the full economic benefits that the flowers have to offer. These observations suggest that plants could also compete for flower-constant foragers by being different from each other, or "difficult" to handle (Heinrich, 1979c).

TO STAND OUT OR TO CONFORM IN INTRASPECIFIC COMPETITION

In the system described above, there should be selective pressure for the flowers of one species to contrast strongly with those of another; each species should be unambiguously identified to the pollinator so that it does not stray. Thus, there is selective pressure for diversity between species and conformity within species. Those individuals that are "different" or that do not conform to the pollinator's search image should suffer a reproductive disadvantage, at least until rewards become limiting and the foragers begin to enlarge their sampling and foraging repertory (Heinrich, 1979a). Selective pressure for conformity within the population presents a potential dilemma, since natural selection acts on the individual and not the group. A seminal paper by Schaeffer & Schaeffer (1979) explores the potential effect of intraspecific competition among Agave as well as Yucca plants for pollinators. The century plant, Agave deserti, produces an inflorescence up to 4 m tall. The pollinators (bumblebees and carpenter bees of Agave, and moths of the genus Tegeticula for Yucca) show preferences for the largest stalks available, and the Schaeffers suggest that this foraging behavior has resulted in the evolution of increasingly greater allocation of resources by the plants to sexual reproduction. Numerous studies indicate that, given a choice between a plant or inflores-

cence with many flowers, or one with few flowers, the pollination unit with more flowers enjoys a greater percentage of pollination per individual flower than the one with fewer flowers (Schaal, 1978; Stevenson, 1979; Augsburger, 1980; Schemske, 1980). If unopposed by a competing selective pressure, one would predict that the floral display would increase to, and possibly beyond, the energetic ability of the plant to support such flowers. The ultimate outcome might be an investment in flowering that is so great that it exhausts the plants' food reserves, and results in the death of the plant following flowering. As suggested by the Schaeffers (1979), this is the strategy that has been adopted by many species

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of *Yucca* and *Agave*; they are highly visible, and individually identifiable by the pollinators, and they literally knock themselves out to attract pollinators.

The limit on the ultimate floral display should be set not by the energy need of the pollinator, but rather by his wants and expectations, which could be considerably higher than his needs. Indeed, the floral reward of some species of Agave are large enough to satisfy not only the energy demands of single bats, but also groups of bats foraging in tight flocks (Howell, 1979). It could be predicted that the plants under the predominating influence of intraspecific competition could ultimately evolve to adopt pollinators with even higher energy expenditure than the bats, or cater to ever-larger flocks of bats that forage as a unit. Such "leap frogging" to adopt progressively larger and energetically more demanding pollinators could be a general evolutionary result of intraspecific competition for pollinators. Massive commitment to a large floral display is also found in the monument plant, Frasera speciosa (Gentianaceae) in the Rocky Mountains (Inouye & Taylor, 1980). This plant also grows in relatively open habitat. Individual plants (inflorescences) that grow to 3 m high are close enough together, however, so that the pollinators (bumblebees) can "compare" and fly to the closest and/or largest neighbor. As in Agave, the plants wait many years before reproducing, and flowering is a massive suicidal commitment of all of their reserves. The plants live 20-62 years before flowering and dying (Inouye & Taylor, 1980).

Unlike the plants described above, there are many species that grow and flower in dense crowds. The pollinators then no longer distinguish flowers on the basis of what individual they belong to. Flowers in crowds will be visited, and pollinated, regardless of whether or not they provide food rewards (Henrich et al., 1977), as long as they are in "good company" (with flowers that *are* rewarding or that have recently been rewarding). Under this situation, it would be selectively advantageous to commit as few resources as possible to nectar production, and to throw the resources into seed production instead. This is, for example, the strategy followed by *Lobelia cardinalis*, a mimic blooming in crowds of other hummingbird-pollinated flowers that are highly rewarding (Brown & Kodric-Brown, 1979). Mimicry that has evolved in the context of intraspecific competition may be relatively conspicuous, but "mimicry" in intraspecific competition may be relatively conspicuous, though far more difficult to detect or demonstrate.

The wider plants grow apart, the more pollinators need to be rewarded to fly long distances between them. It is therefore not surprising that most of the highenergy pollination systems are in the tropics, where because of seed predation (Janzen, 1970) and high species numbers, plants are spaced far apart. Conversely, the closer plants are together, the less rewards are needed to feed the pollinators. Furthermore, if the plants are close enough together in a crowd and the pollinator no longer discriminates between individuals, the presentation of rewards should become no longer necessary by individual plants. As explored elsewhere in more detail (Heinrich, 1980), the plant could then either go extinct for lack of pollinators, become autogamous, or become wind pollinated. Most angiosperm plants that are now wind pollinated had insect-pollinated ancestors (Whitehead, 1969). Charles Darwin (1878), who speculated on the evolution of wind pollination,

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suggested that it evolved in temperate regions due to scarcity of pollinators. However, there is little evidence for numerical lack of insects in the temperate regions, but if there were a lack of pollinators, then this could as readily be an effect of low nectar availability from the plants, rather than a cause for wind pollination.

It must be noted, however, that no one scheme likely always functions to the exclusion of all others. For example, changes of reward within single flowers with many nectaries, or in inflorescences with many flowers, could affect pollination of these flowers. Bumblebees visit and touch inflorescences of clover only briefly, or not at all, if they contain minute nectar rewards, but they stay to visit nearly a dozen florets (as opposed to only 2 or 3), twirling about the inflorescence if the florets contain their full complement of nectar (Heinrich, 1979b), thus presumably transferring more pollen to the flowers. Can we make broad generalizations in pollination biology? The diverse examples given should perhaps be taken to have interest in their own right. It is clear that no simple models will suffice to explain all of the complexities in any one instance. Good simple models, however, can be abstracts of realities that may or may not apply, or that apply to varying degrees, with specific examples. The selective pressure for any one trait may be multiple and parallel, or they may be conflicting. The range of possibilities, which are not mutually exclusive to account for specific results, are wide.

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